

Influence of climatic gradients on metacommunities of aquatic invertebrates on granite outcrops in southern Western Australia

B V TIMMS

Australian Wetlands and River Centre, School of Biology, Earth and Environmental Sciences,
University of New South Wales, NSW 2052, Australia. ✉ brian.timms@unsw.edu.au

Some 210 pools on 21 rock outcrops arranged along two climatic gradients were surveyed for invertebrates in the winter–spring of 2010 and 2011. Almost all pools had clear fresh waters and most were near-full when sampled. Ninety-three taxa were identified, with crustaceans and insects about equally represented; crustaceans were numerically dominant, particularly *Limnadia badia*, *Boeckella opaquia* and *Cypericercus* spp. Individual rock metacommunities ranged from 19 to 35 species, with notable decreases along a southwest–northeast climatic gradient, but little decrease along an east–west transect where climatic changes were less. Species richness was also influenced by the relative number of pools on each rock, with two saline pools added to one rock's metacommunity causing an anomaly. Diversity of cladocerans decreased most along the gradients with ostracods next and insects hardly affected. The most important influencing factor is hydroperiod which is largely determined by an interaction between rainfall and evaporation. In stress years such as 2010, these are reduced and some species may not complete their life cycle. Future climate change may act to reduce hydroperiods, particularly at northern and northwest fringes of the Wheatbelt and Goldfields.

KEYWORDS: aquatic insects, branchiopods, cladocerans, climate, gnammas, hydroperiod, ostracods.

INTRODUCTION

In recent decades there have been a number of studies on rock pools (pan gnammas *sensu* Twidale & Corbin 1963) on granite outcrops in southern Western Australia, focused on the Wheatbelt and adjacent Goldfields regions (Bayly 1982, 1997; Pinder *et al.* 2000; Jocqué 2007; Timms 2006, 2012; Jocqué *et al.* 2007). Overall, they reported a rich aquatic fauna, with a large endemic crustacean component. Individual pools are small and rocks isolated so any pool or set of pools supports only part of the total metacommunity known to occur in gnammas (Jocqué *et al.* 2010). As well as each pool/pool set having a variable composition due to stochastic events and local environmental factors, there is evidence of regionalisation of the fauna (Timms 2012). The Northcliffe pools (near the coast in far southwestern Australia) studied by Bayly (1982) have but a small subset of species common across the Wheatbelt and moreover there is a decline in species richness in Wheatbelt transects south-southeast to north-northwest (Jocqué 2007; Timms 2012). It is possible both differences could be associated with climatic influences expressed mainly in hydroperiod lengths determined by the interaction of seasonal rainfall and evaporation. In addition, different energy pathways in the Northcliffe pools could be contributing factors (Bayly 1982; Timms 2012).

It is likely there are other differences between pool groups in different districts, with field experiences suggesting widespread lower species richness in gnammas at the western and southern fringes of the Wheatbelt and towards the Goldfields and non-

agricultural land to the north and northeast, as well as metacommunity differences in rock pools near the coast. As in the case of the Northcliffe series, those on rocks at the eastern fringe at the Arid Woodland – Nullarbor interface, namely at Balladonia, seem to have some species not found elsewhere (Timms 2006). It is the aim of this study to examine pools on rocks on the northeast and eastern edges of the Wheatbelt and onwards to the Mulga association in the north and Arid Woodland in the east in order to detect differences in diversity and species composition from that pertaining in the area of perceived maximum diversity near Hyden. Although diversity may be a little higher to the south of here (e.g. at Mt Madden: Timms 2012), the Hyden area's gnammas are the best studied and so provide a suitable reference area. It is possible other factors such as pool size, numbers and salinity influence metacommunity diversity (Jocqué *et al.* 2010; Vanschoenwinkel *et al.* 2009; Waterkeyn *et al.* 2008), so note will be taken of these.

METHODS

Pan gnammas vary greatly in size, although generally the pools are shallow (<25 cm deep), flat floored, somewhat circular and <5 m in diameter (Twidale & Corbin 1963; Timms 2012). The rock outcrops containing them are highly variable both in size and elevation above the surrounding plain and also the number of pools per outcrop varies widely.

The present study is concerned with transects in different directions, one to the northeast and one to the east of Hyden: the first across a rainfall gradient of 342–250 mm mean annual rainfall and 350 km long, and the second parallel to isohyets once east of Hyden and in a similar rainfall regime of ~260 mm annual rainfall (264

mm at Norseman and 263 mm at Balladonia) (Figure 1) and extending beyond the Arid Woodlands of the southern Goldfields to the edge of the Nullarbor, a distance of 560 km.

In this study of rock outcrops along two transects, three rocks in each area were chosen instead of one (as in Jocqué 2007 and Timms 2012) in order to facilitate comparisons statistically. In establishing a transect, granite rock outcrops should ideally be equidistant apart, be equal size and shape, and have equal numbers of similarly sized pools. This was not always possible because of environmental heterogeneity, but nevertheless a measure of homogeneity was achieved. Rock areas averaged 133 km apart with greatest irregularity caused by the Norseman set (rocks 13–15) only 95 km away from the Johnson set (10–12) and 200 km from the Balladonia set (16–18). Rock outcrops varied from being compact and well elevated (e.g. King Rocks, McDermid Rocks) to being of broken exposure and virtually at surrounding ground level (e.g. Afghan Rocks, Old Rainey Rocks), but these differences were not thought significant. Of more importance is the number of pools per rock, as this could influence species richness in a rock pool set (B Vanschoenwinkel pers. comm. 2012); while most rock outcrops had 50–100 pools, some had only a few more than those sampled (e.g. Ularring Rock with 15) or many more (e.g. Hospital Rocks with > 200) (Table 1). Ten pools were sampled per rock, a number which gives an acceptable representation of aquatic diversity (Pinder *et al.* 2000; Jocqué *et al.* 2007; Timms 2012). Because species richness is influenced by pool size (Vanschoenwinkel *et al.* 2009) it was important to use a standard ratio of small (<1.9 m) diameter to medium (2–5 m) and large (>5.1 m). The ratio of 2:6:2, small/medium/large, was chosen because medium-sized pools were the most common on

almost all the rocks chosen. Generally, the average diameter for each pool set on each rock was between 4 and 5 m (Table 1), though median values were 1–1.5 m lower because averages were skewed by some very large pools (10–20 m diameter). Ularring Rock had unusually small pools and Hospital Rocks had the biggest pools (Table 1). Field work was in August and early September when pools are generally at or near maximum depths and have maximal biotic diversity (Timms 2012). The range of individual pool depths was 5–36 cm, the lower value by design (pools <5 cm depth were rejected) and most averages were between 6 and 14 cm. Most rocks were visited in 2011, with some data extracted from an earlier study in 2010 (Timms 2012). While almost all rocks were visited just once, some longer term comparative data are available for the Balladonia series (rocks 16–18) (B V Timms unpubl. data), for Hyden and King Rocks (Jocqué *et al.* 2007), and seasonal data for the five rocks on a north-northwest–south-southeast transect (Timms 2012).

Sampling protocol was similar to that used by Timms (2012) on five rocks on a north-northwest transect used as comparative data in this study. Pool water depth was determined with a stiff tape measure at the deepest point to the nearest centimetre and pool size was estimated with the same tape by measuring two cross sections at right angles to nearest 5 cm. Conductivity was measured with a Hanna HI8733 meter, and general observations made on turbidity using a Waterwatch turbidity tube.

Two different nets were used to sample the fauna. A small plankton net, aperture 15 x 10 cm, 30 cm long and of mesh 159 µm, was used to sample microfauna in the water column and on the bottom (the latter by disturbing the sediment and then passing the net through the

Table 1 Rocks studied, location, size and number of pools.

No.	Rock name	Rock set name	Coordinates	Date visited	Average diameter of pools (m)	Average depth of pools (cm)	No. of pools
1	Hyden Rock	Hyden	32°26'44"S, 118°54'14"E	1 Aug 2010	4.16	10.8	~50
2	Anderson Rocks	Hyden	32°10'03"S, 118°51'11"E	26 Aug 2010	3.84	8.5	~100
3	King Rocks	Hyden	32°19'00"S, 119°09'09"E	27 Aug 2010	5.74	14.2	~100
4	Boondi Rock	Highway	31°10'45"S, 120°22'56"E	4 Aug 2011	5.95	12.6	~50
5	Boorabin Rock	Highway	31°12'13"S, 120°17'20"E	4 Aug 2011	4.65	13.4	~50
6	Karalee Rocks	Highway	31°09'47"S, 120°32'55"E	5 Aug 2011	4.82	10.6	~100
7	Old Rainey Rocks	Menzies	29°43'37"S, 119°37'25"E	5 Aug 2011	3.38	7.5	~25
8	Hospital Rocks	Menzies	29°50'20"S, 120°07'06"E	6 Aug 2011	8.73	12.7	~200
9	Ularring Rocks	Menzies	29°55'32"S, 120°32'56"E	6 Aug 2011	4.04	9.5	~15
10	McDermid Rock	Johnson	32°01'16"S, 120°44'13"E	30 Aug 2011	4.36	10.4	~75
11	Banks Rock	Johnson	31°55'48"S, 120°15'58"E	31 Aug 2011	4.75	10.9	~40
12	Disappointment Rock	Johnson	32°07'56"S, 120°55'38"E	31 Aug 2011	3.92	6.7	~15
13	McPherson Rocks	Norseman	32°27'10"S, 121°40'28"E	1 Sep 2011	4.22	6.0	~20
14	Unnamed rocks	Norseman	32°24'56"S, 121°40'51"E	2 Sep 2011	3.81	5.5	~40
15	Theatre Rocks	Norseman	32°08'25"S, 121°33'23"E	2 Sep 2011	4.73	5.3	~40
16	Afghan Rocks	Balladonia	32°21'23"S, 123°40'05"E	3 Aug 2011	5.67	8.0	~40
17	Booanya Rock	Balladonia	32°45'38"S, 123°36'27"E	2 Aug 2011	5.56	9.7	~30
18	Balladonia Rock	Balladonia	32°27'39"S, 123°51'52"E	2 Aug 2011	3.15	7.9	~20
19	Mt Madden	–	33°14'23"S, 119°50'34"E	1 Aug 2010	4.12	10.7	~150
20	Yanneymoon Rock	–	30°42'50"S, 118°33'19"E	2 Aug 2010	4.13	6.8	~120
21	Bullamunya Rocks	–	29°09'51"S, 117°39'40"E	3 Aug 2010	5.01	5.5	~150
22	Walga Rock	–	27°24'14"S, 117°27'49"E	8 Sep 2010	4.00	9.8	~20

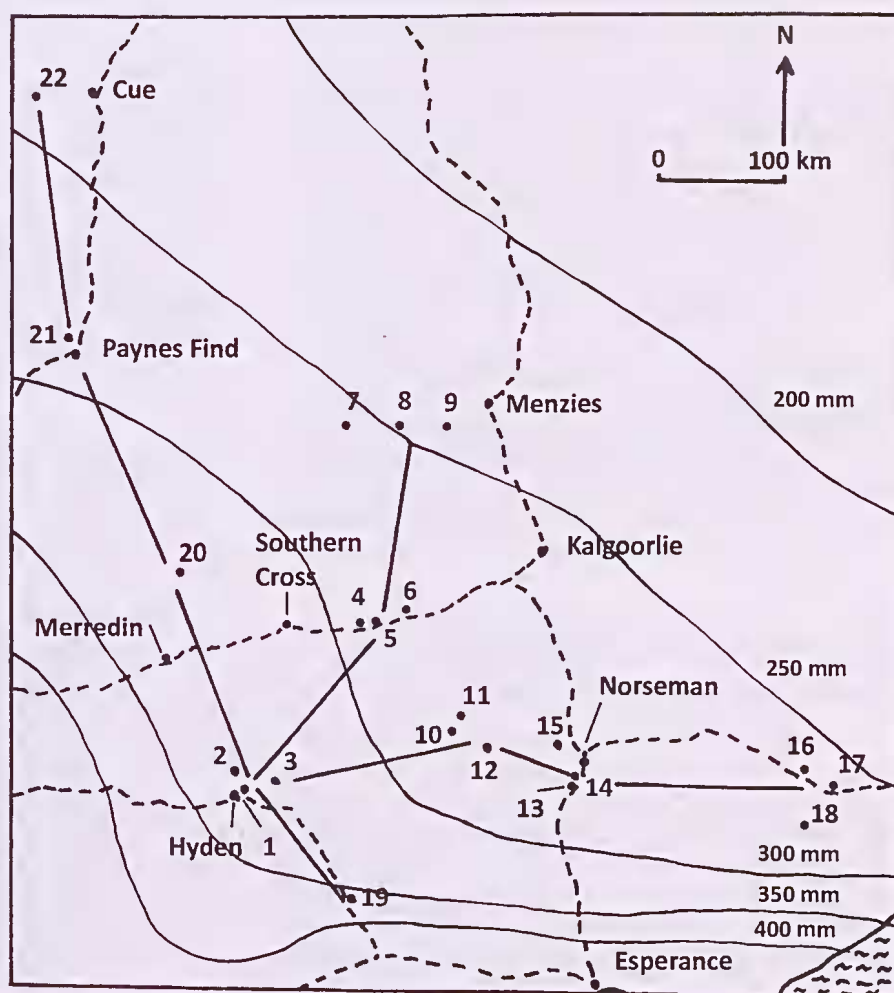
slurry). A household sieve, 20 cm in diameter and of mesh size ~2 mm was used for larger invertebrates. The number (5–20) of sweeps of each device was adjusted to pool size so that about 50% of the water volume in small pools was sampled down to 5% in the very large pools. This introduced an error between pools in estimating abundance and species richness, but the bias was constant between rocks.

Plankton were concentrated by settling first in dilute ethanol, then pouring off the supernatant and preserving in >70% ethanol. Sieve collections were handpicked in the field from a sorting tray; one individual (a few of more abundant chironomids) of each species was kept and preserved in 70% ethanol and the remainder returned alive to the pond. In the laboratory each plankton collection for each pool was examined completely under an Olympus SZ61 stereomicroscope, species identified and the number of each species estimated on a log scale. The number of macroinvertebrates caught in the sieve was also estimated on a log scale. In both cases an index of abundance of each species in the 10 pools was calculated by adding abundances in each pool. Also in determining species richness for a rock, beetle larvae are not counted unless the adults were not recorded.

The term metacommunity is here used in two senses: to describe the whole set of animals found on an individual rock [the community in each pool contain only a subset of the animals living in all pools on a rock (Vanschoenwinkel *et al.* 2007; Jocqué *et al.* 2010)] or to describe the communities living on three rocks close to one other. The rocks studied were chosen to form six sets: Hyden, Highway and Menzies on the northeastern transect and Hyden, Johnson, Norseman and Balladonia on the eastern transect (Figure 1; Table 1).

Statistical differences between rock areas were tested with two tailed t-tests. Relationships between assemblages on the five rocks were investigated using PRIMER (v5) (Clarke & Gorley 2001). For the north-northwest transect the average seasonal abundance data of invertebrates from the mid-July, early and late August and mid-September trips (Table 1) was log (N+1) transformed prior to multivariate analysis. In the northeastern and eastern transects the data collected on the single visits was similarly transformed prior to analysis. Non-metric multidimensional scaling, based on the Bray–Curtis similarity index was used to represent assemblage composition in two-dimensional space. Relative distance apart in the ordination represents relative dissimilarity.

Figure 1 Map of study area in inland Western Australia. Rock outcrops 1 to 22 as in Table 1. Three transects shown: north-northwestern from 19 to 22 (from Timms 2012), northeastern from 1,2,3 to 7,8,9, and eastern from 1,2,3 to 16,17,18. Major towns and roads and smoothed isohyets shown.



RESULTS

Most pools were full or near full when sampled as there had been adequate rainfall in the previous weeks. Conductivities were $<200 \mu\text{S/cm}$ and often $<75 \mu\text{S/cm}$ in all pools except two. Both exceptions were deeply incised pools on Booanya Rock, one with a conductivity of $4200 \mu\text{S/cm}$ and the other a conductivity of $9000 \mu\text{S/cm}$; in both pools staining of the rocks suggested no overflow ever. All pools had turbidities less than 15 NTU, often lower, so that their floors were always visible.

The eastern transect yielded 78 taxa of invertebrates and the northeastern transect had 65 taxa (Appendices 1, 2), making 93 together. If full identifications were possible, the lists would be about 5% longer as a few taxa are thought to be comprised of two or more species. Dominant taxa on most rocks included *Limnadia badia*, *Boeckella opaqua* and *Cypericercus* spp. Other common species across many rocks or particularly common on just a few rocks were two unidentified planarians, *Branchinella longirostris*, *Caenestheriella mariae*, *Ceriodaplnia* sp., *Ilyodromus amphicolis*, *Stenopriscus multimaculatus* and *Paraborniola tonnoiri*. While crustaceans and insect species were similarly diverse on most rocks, it was the crustaceans which were by far the most numerous (Appendices 1, 2)

Momentary species richness (MSR) on individual rocks ranged from 19 to 35 species, with averages per rock set varying from 22.3 to 32.3 (Figure 2; Table 2). There was a small decrease in species richness from west to east along the eastern transect and a much larger decrease along the northeastern transect (Figure 2). Decrease eastwards along transects was due mainly to cladocerans and to a lesser extent to ostracods; insects remained just as diverse northeastwards and actually increased mid-length along the eastern transect (Figure 3). These changes were only significant between the Hyden and Highway rock sets, Hyden and Menzies sets and between the Johnson and Menzies rock sets (Table 3), thus confirming the distinctiveness of the two outlying northeastern sets.

Three rock sets had higher coefficient of variations than the others, due to one or more of the rocks having markedly higher or lower MSRs (Table 2). In the Menzies set, Hospital Rocks were most speciose coincident with this rock having many more pools than the other two; on the other hand in the Johnson set, Disappointment Rock was less speciose than its two nearby rocks coincident with this rock having comparatively fewer pools. In the

case of the Balladonia set, Booanya Rock was most speciose, possibly associated with it having two saline pools and hence some species unique to it. Also in this the most variable of all sets, Balladonia Rock had the lowest species richness and coincidentally it had the fewest pools.

Distinctiveness of rock sets was even greater when explored using Bray–Curtis dissimilarities to create a multidimensional ordination (Figure 4). Rocks within sets were clumped closer together than between sets, indicating a strong geographical influence on pool fauna. Among the rock sets there were large distances between the three sets on the northeastern transect, but on the eastern transect the Johnson and Norseman sets clumped nearer each other and to the Hyden set while the Balladonia set was the most divergent of all. While some of this inequality is explained by the geographical closeness of the Johnson and Norseman sets and remoteness of the Balladonia set (see Figure 1), the Balladonia set contained a few species unique to it, including *Branchinella spinosa*, *Triops* n. sp., *Daplinoopsis queenslandicus*, *Cabanocypris nunkeri* and *Heterocypris* sp. By contrast the other outlying sets had largely somewhat depauperate associations of species compared to the richer Hyden set (Appendices 1, 2).

DISCUSSION

Species richness figures for pools on rock outcrops depend on the collection methods and especially the number of pools sampled, either momentary or cumulative with time. For instance at Wave Rock the cumulative species count was still increasing even after 57 pools were sampled (Jocqué *et al.* 2007). Sampling such a large number of pools takes days and so is impractical, so generally studies sample just 10 pools, but this catches only about 80% of the species comprising the metacommunity and samples from just a few pools per rock catch an even lower percentage of species, e.g. five pools yielded ~50% of the species at Wave Rock (Jocqué *et al.* 2007). Regular seasonal studies add more species: e.g. at Wave Rock the present study reports 30 species, yet Timms (2012) found 41 species in a seasonal study,

Table 3 t-tests on differences in MSR between grouped sites (significant values in bold).

Rock sets	P value
Hyden & Johnson	0.898
Hyden & Norseman	0.111
Hyden & Balladonia	0.257
Johnson & Norseman	0.270
Johnson & Balladonia	0.333
Norseman & Balladonia	0.916
Hyden & Highway	0.026
Hyden & Menzies	0.034
Highway & Menzies	0.224
Johnson & Highway	0.135
Johnson & Menzies	0.038
Norseman & Highway	0.272
Norseman & Menzies	0.104
Balladonia & Highway	0.598
Balladonia & Menzies	0.165

Table 2 Species richness on the 6 rock sets.

Rock set	Value 1	Value 2	Value 3	Mean	SD	SE	C of V
Hyden	30	33	34	32.3	2.08	1.2	0.064
Johnson	35	33	28	32	3.61	2.08	0.113
Norseman	26	30	30	28.7	2.31	1.33	0.080
Balladonia	28	24	33	28.3	4.51	2.6	0.159
Highway	26	28	26	26.8	1.15	0.66	0.049
Menzies	19	27	21	22.3	4.16	2.4	0.186

Note that with a rock set, the richness values represent rocks in the order they are given in Table 1.

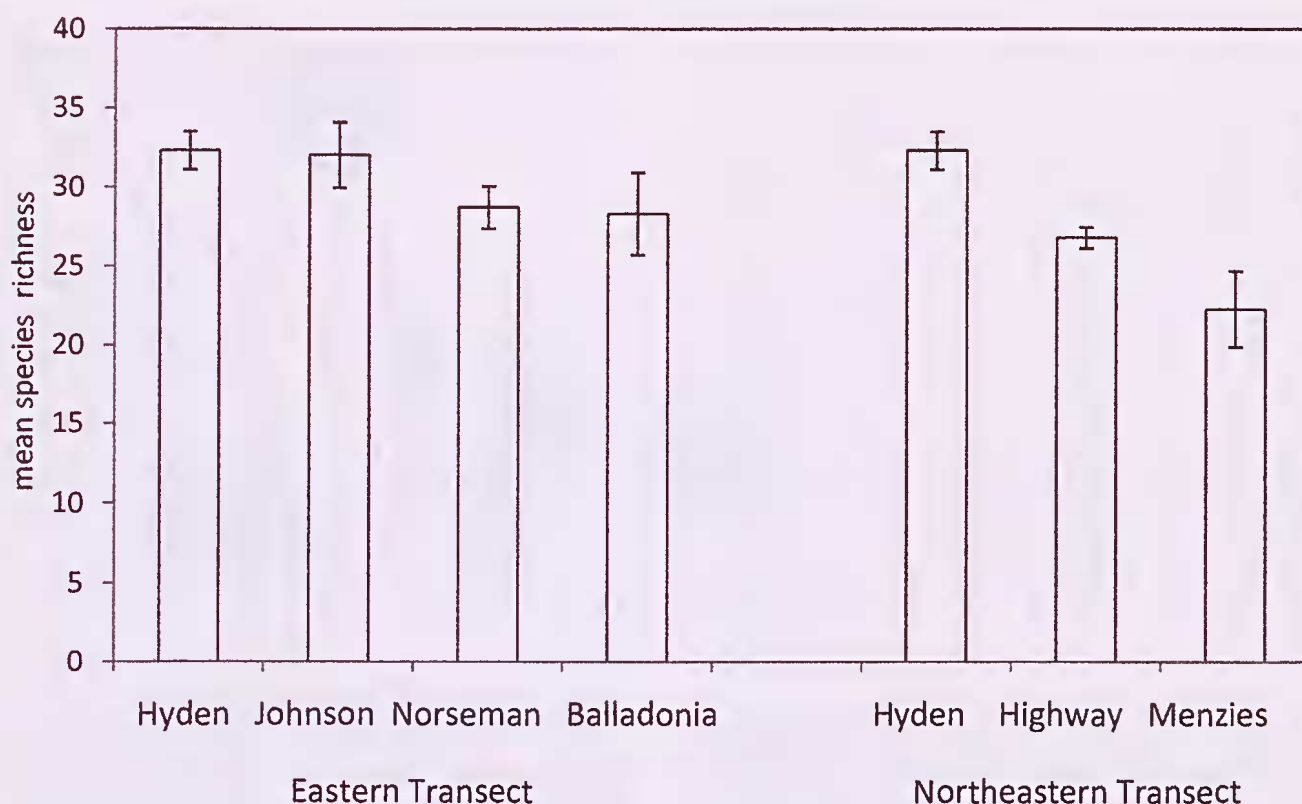


Figure 2 Number of species in metacommunities along the northeastern and eastern transects.

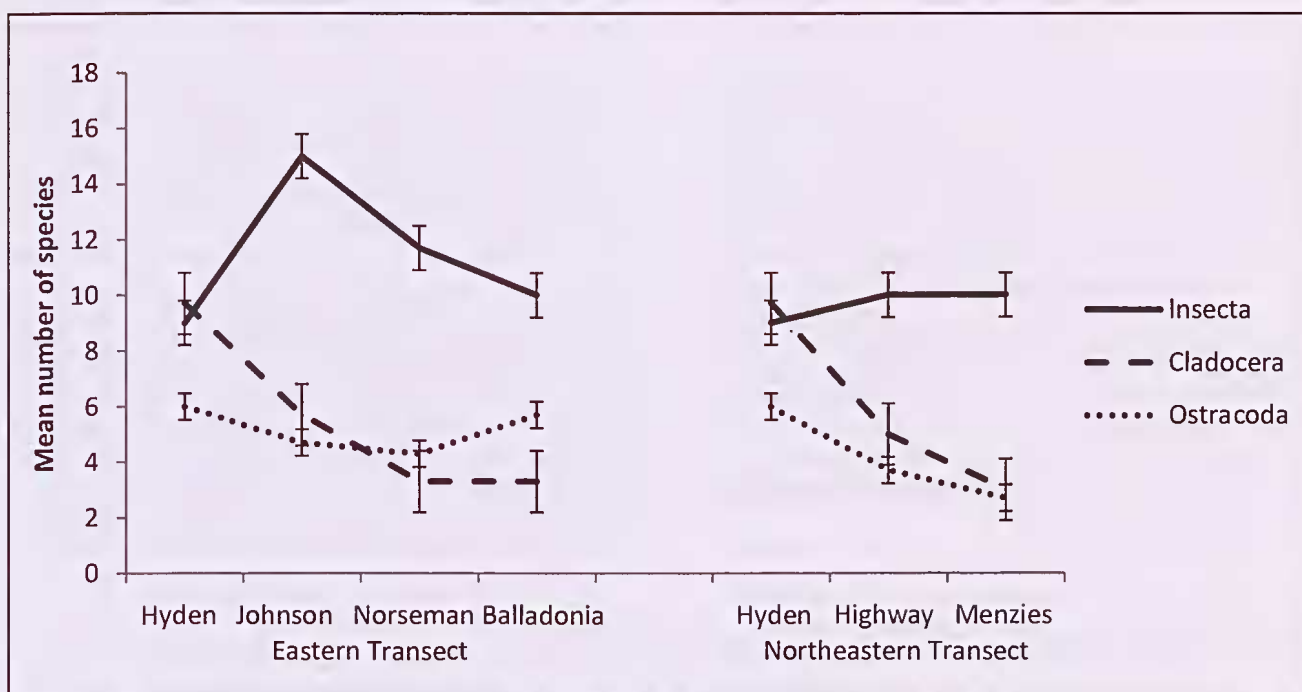


Figure 3 Changes in the number of insects, cladocerans and ostracods along the northeastern and eastern transects.

using exactly the same collecting methods. Studies over many years can further extend lists, with the list for Balladonia increasing from 24 in this study to 33 over three years and with some species varying greatly in numbers from year to year (B V Timms unpubl. data). Hence in comparing data it is important to know the number of pools sampled and how often.

The extensive and detailed study by Pinder *et al.* (2000) of about 10 pools on each of nine rock outcrops and the survey of 36 pools by Bayly (1997) across the Wheatbelt revealed a weak areal pattern in metacommunities across the Wheatbelt, though the large branchiopod component showed no significant distributional pattern across the Wheatbelt and adjacent

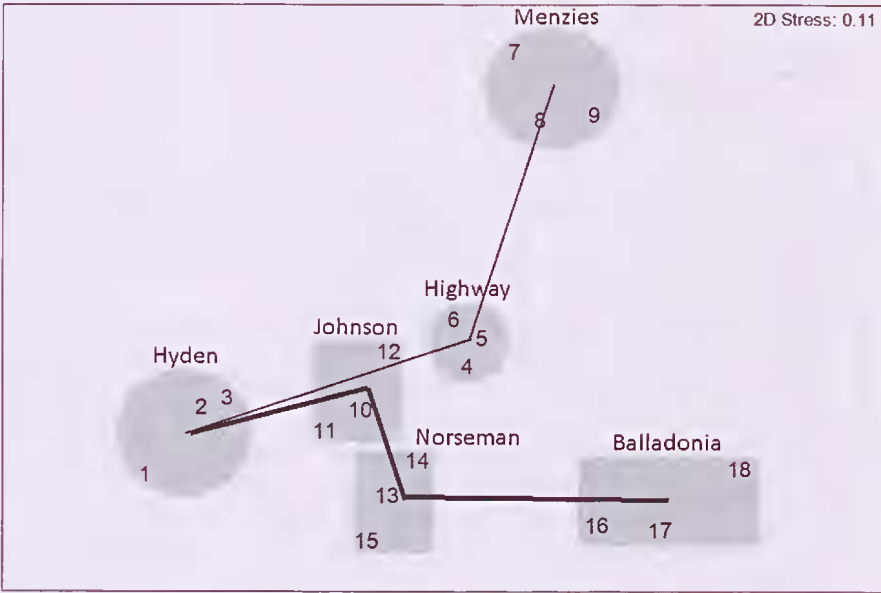


Figure 4 Ordination diagram of the relationships between rock sets along the northeastern transects (thin line) and eastern transects (thick line). Individual rock numbers as listed in Table 1.

Goldfields (Timms 2006). However an examination of Bayly (1982), who studied rock pools near Northcliffe, near Albany and southeast of Perth (i.e. pools in coastal forests), revealed a restricted fauna compared to that in the Wheatbelt. Six Northcliffe pools had a metacommunity of just 13 species and lacked large branchiopods, insects and planarians and had only two ostracod and five cladoceran species. Seven pools southeast of Perth yielded 16 species, almost all common throughout the Wheatbelt, but nevertheless a depauperate metacommunity compared to those on Wave Rock and King Rocks (Jocqué *et al.* 2007). Following on from an indication of differences between metacommunities in the northern, central and southern Wheatbelt (Pinder *et al.* 2000), in a north-northwest-south-southeast transect 700 km long from Wave Rock (near Hyden) to Walga Rock (west of Cue) (Figure 1), Jocqué (2007) noted a significant decrease in generic richness northwards with the metacommunities differing significantly from each other, with 26.7% of the variance explained by precipitation differences between north and south. More detailed studies along a similar transect (but with a slightly different array of rock outcrops), showed a similar decrease in species richness northwards (Table 4) (Jocqué 2007; Timms 2012).

In the present study, the decrease in species richness along the northeast transect is less than on the longer north-northwest transect of Jocqué (2007) and Timms (2012), and minimal on the eastern transect (Figure 2; Table 4). In that all three transects terminate in areas with ~250 mm rainfall, environmental factors other than rainfall annual averages may be influential. Two important ones could be evaporation and rainfall reliability. Annual evaporation is much greater at the northern terminus (~3000 mm at Cue) than at the northeastern Menzies terminus (2800 mm) and least at the eastern Balladonia terminus (2000 mm) (all figures estimated from Bureau of Meteorology 2012a). Such differences mean that pool water persists much longer further south and hence fauna have a better chance of completing life cycles at southern sites. Rainfall is almost twice as reliable in the south at Balladonia than at Cue, with Menzies intermediate (Gaffney 1975). Again, but over a longer term, rainfall unreliability might adversely influence metacommunities in the north by disrupting life cycles and by reducing survivorship of propagules (Boulton & Lloyd 1992; Jenkins & Boulton 2007). For instance the drought year of 2010 was far more disruptive of life cycles at Walga Rock in the north than at rocks in the south (Timms 2012). These are aspects of

Table 4 Data on variation in metacommunities along a NNW-SSE transect.

	Mt Madden	Hyden Rock	Jilbadgie Rock	Beladgie Rock	Elach- butting	Remlap Rock	Bullamanya Rocks	Walga Rock
Jocqué (2007)								
Generic richness	–	33	30	24	22	37	20	13
Timms (2012)					Yanney- moonong			
Insecta	17	17	–	–	14	–	16	10
Cladocera	15	13	–	–	11	–	12	0
Ostracoda	8	7	–	–	6	–	7	2
Total spp.	51	41	–	–	41	–	37	16

the overall hydroregime, a factor of paramount importance in influencing community structure of rock pools (Vanschoenwinkel *et al.* 2009).

A multiple regression of the above three factors gave the equation:

$$SR = 28.48 + 53.68x - 74.23y - 5.79z$$

where SR is species richness, x is rainfall in metres, y is evaporation in metres and z is a reliability factor based on coefficient of variation (Cowling *et al.* 2005). The equation explained 85% of the variance. From this, all three factors are influential (and rainfall and evaporation are significant at 05% level individually, with rainfall reliability significant at the 10% level). Evaporation needs to be added to rainfall as a factor influencing hydroperiod and hence species richness in pools. Rainfall reliability is most likely acting through differential survivorship of propagules, but no work has been done on species inhabiting gnammas.

Other factors influencing species richness in the present rock sets include the unique additional presence of saline species at Booanya Rock which elevate species richness in the Balladonia rock set (no other saline gnammas are known in southwest Western Australia: Bayly 1982, 1997; Jocqué *et al.* 2007; Pinder *et al.* 2000; Timms 2012). Probably also of influence is the total number of rock pools on each rock outcrop, increased numbers allowing for more colonisation and survival of species on a rock (B Vanschoenwinkel pers. comm. 2011). While every effort was made to standardise this factor's influence in this study, it seemed to affect species numbers positively on Hospital Rocks compared to other Menzies rock set, and negatively on Disappointment and Balladonia Rocks compared to other rocks in their respective sets. Interestingly Pinder *et al.* (2000) had lower species richness than average on rocks (Styles near Grass Patch, Punaputin near Wagin) which I know have few pools compared to other rocks they studied.

Of the various taxonomic groups represented in gnammas, the most important are large branchiopods, cladocerans, ostracods and various insects. Insects are least affected by environmental factors associated with climatic factors, diversity being only slightly less in pools on rocks in the harsher north and northeast (Figure 3; Table 3). The reason for this may lie in insects being active dispersers and also being largely unaffected by hydrology of the pools. Exceptions include some chironomids, but *Paraborniola tonnoiri* and *Allotrissoidea* spp have special life cycle adaptations to survive in temporary pools (Edward 1968; Jones 1971). The absence of insects in the Northcliffe pools and their scarcity in the forest gnammas east of Perth is less easy to explain, but there may be many other suitable habitats nearby which harbour them whereas suitable habitats in the remote inland are scarce, gnammas being the main reliable water and hence particularly attractive to dispersing insects. There are too few large branchiopod species to plot in Figure 3, but they are widely distributed in rock pools across the Wheatbelt and Goldfields (Timms 2006), though less conspicuous in the gnammas in forests near Perth and absent from the Northcliffe pools. Either the markedly acidic nature of these pools is inimical to large branchiopods or their food or perhaps eggs do not

readily disperse eastwards against the prevailing southwesterly winds.

It is the cladocerans and ostracods that are most affected by the imposition of harsher climatic factors of the north, northeast and far east of the Wheatbelt–Goldfields of southern Western Australia (Figure 3; Table 4). The increase in richness of ostracods on the eastern transect is an anomaly and is due to the addition of saline species at Booanya rock. Most data suggest that the majority of species can withstand a range of hydrological conditions so that diversity decreases only slowly northwards and it is only in the remote goldfields or far east on the Nullarbor fringe that many species are absent. Common species living in a wide variety of hydrological conditions include *Limnadia badia*, *Boeckella opaquia*, *Macrothrix hardingi* and most of the insects. Notable absences of cladocerans from remote areas include *Ceriodaphnia* n. sp., *Daphnia jollyi*, *Leberis aenigmatica*, *Planicirculus alticarinatus* and *Plurispina* sp. No species of ostracods can be identified in this decrease, partly because they are less well known taxonomically but overall they may be more resilient than cladocerans.

Climate is changing and already over the last 41 years rainfall has decreased 2–10% in much of the wheatbelt (Bureau of Meteorology 2012b), though it is not known if this has affected invertebrate communities in rock pools by shortening hydroperiods. For most of the Wheatbelt it probably has not, as all crustaceans and almost all insects completed their life cycles in the drought year of 2010 at all rocks except at the most northern site, Walga Rock (Timms 2012). However a predicted further decrease of 2–5% in annual rainfall in southern Western Australia (Bureau of Meteorology 2012b) may at least curtail hydroperiods in the drier areas, disrupt life cycles and hence adversely affect diversity. The evidence for the most northern site, Walga Rock suggests the species list was almost exactly the same in 2009 (M Jocqué unpubl. data) as it was in the drought year of 2010 (Timms 2012), the difference between the two years being in the failure of many species to complete their life cycles in 2010. How often this can occur before local extinction takes place is not known and it is possible that some species still common further south may have already succumbed in the far north.

ACKNOWLEDGEMENTS

I thank the Bayly and Trenorden families for hospitality, taxonomists as listed in Timms (2012) plus Ros St Clair for Trichoptera, and Ian Bayly, Bram Vanschoenwinkel and Journal reviewers Adrian Pinder and Neville Marchant for helpful comments on the manuscript.

REFERENCES

- BAYLY I A E 1982. Invertebrates of temporary waters on granite outcrops in southern Western Australia. *Australian Journal of Marine and Freshwater Research* 33, 599–606.
- BAYLY I A E 1997. Invertebrates of temporary waters in gnammas on granite outcrops in Western Australia. *Journal of the Royal Society of Western Australia* 80, 167–172.
- BOULTON A J & LLOYD L N 1992. Flooding frequency and invertebrate emergence from dryland sediments of the River

- Murray, Australia. *Regulated Rivers: Research and Management* 7: 137–151.
- BUREAU OF METEOROLOGY 2012a. www.bom.gov.au/wat1/evaporation (accessed 16 April 2012).
- BUREAU OF METEOROLOGY 2012b. www.bom.gov.au/climate/change (accessed 16 April 2012).
- CLARKE K R & GORLEY R N 2001. PRIMER v5: user manual/tutorial. PRIMER-E, Plymouth.
- COWLING R M, OJEDA F, LAMONT B B, RUNDEL P W & LECHMERE-OERTEL R 2005. Rainfall reliability, a neglected factor in explaining convergence and divergence of plant traits in fire-prone Mediterranean-climate ecosystems. *Global Ecology and Biogeography* 14, 509–519.
- EDWARD D H D 1968. Chironomidae of temporary freshwaters. *Australian Society for Limnology Newsletter* 6, 3–5.
- GAFFNEY D O 1975. Rainfall deficiency and evaporation in relation to drought in Australia. Presented to 46th ANZAAS Congress, Canberra 1975, Bureau of Meteorology, Melbourne.
- JENKINS K M & BOULTON A J 2007. Detecting impacts and setting restoration targets in arid-zone rivers: aquatic micro-invertebrate response to reduced floodplain inundation. *Journal of Applied Ecology* 44, 823–832.
- JOCQUÉ M 2007. Community structuring processes in temporary freshwater rock pools. PhD thesis, Katholieke Universiteit, Leuven (unpubl.).
- JOCQUÉ M, TIMMS B V & BRENDONCK L 2007. A contribution on the biodiversity and conservation of the freshwater fauna of rocky outcrops in the central Wheatbelt of Western Australia. *Journal of the Royal Society of Western Australia* 90, 137–142.
- JOCQUÉ M, VANSCHOENWINKEL B & BRENDONCK L 2010. Freshwater rock pools: a review of habitat characteristics, faunal diversity and conservation value. *Freshwater Biology* 55, 1587–1602.
- JONES R E 1971. The ecology of some species of Diptera on granite outcrops. PhD thesis, University of Western Australia, Perth (unpubl.).
- PINDER A M, HALSE S A, SHIEL R J & MCRAE J M 2000. Granite outcrop pools in south-western Australia: foci of diversification and refugia for aquatic invertebrates. *Journal of the Royal Society of Western Australia* 83, 149–161.
- TIMMS B V 2006. The large branchiopods (Crustacea: Branchiopoda) of gnammas (rock holes) in Australia. *Journal of the Royal Society of Western Australia* 89, 163–173.
- TIMMS B V 2012. A seasonal study of aquatic invertebrates in five sets of latitudinally separated gnammas in southern Western Australia. *Journal of the Royal Society of Western Australia* 95, 13–28.
- TWIDALE C R & CORBIN E M 1963. Gnammas. *Revue de Géomorphologie Dynamique* 14, 1–20.
- VANSCHOENWINKEL B, DE VRIES C, SEAMAN M & BRENDONCK L 2007. The role of metacommunity processes in shaping invertebrate rock pool communities along a dispersal gradient. *Oikos* 116, 1255–1266.
- VANSCHOENWINKEL B, HULSMAN A, DE ROECK E, DE VRIES C, SEAMAN M & BRENDONCK L 2009. Community structure in temporary rock pools: disentangling the effects of habitat size and hydroregime. *Freshwater Biology* 54, 1487–1500.
- WATERKEYN A, GRILLAS P, VANSCHOENWINKEL B & BRENDONCK L 2008. Invertebrate community patterns in Mediterranean temporary wetlands along hydroperiod and salinity gradients. *Freshwater Biology* 53, 1808–1822.

Received 20 June 2012; accepted 4 September 2012

APPENDIX 1 SPECIES LISTS FOR ROCKS ON NORTHEASTERN TRANSECT

Major group	Species	Hyden	King	Anderson	Boondi	Boorabin	Karalee	Old Rainey	Hospital	Ularring
Turbellaria	unidentified black planarian	xx	xx	xx	xx	xx	xx	xx	xx	xx
	unidentified green planarian	xx	x	x	-	-	-	-	-	-
	Unidentified rhabdocoel	-	-	o	-	-	-	-	-	-
Nematoda	unidentified nematodes	xx	xx	xx	x	o	o	xx	x	o
Branchiopoda	<i>Branchinella longirostris</i>	r	o	x	x	-	x	-	xxx	x
	<i>Linnadia badia</i>	xx	xx	xx	xxx	xx	xx	xx	xxx	xx
	<i>Caenestheriella mariae</i>	-	o	-	x	x	x	-	-	-
	<i>Daphnia johyi</i>	-	x	-	x	x	x	-	-	-
	<i>Ceriodaphnia</i> sp.	xxx	xxx	xxx	-	-	o	-	-	-
	<i>Moina australiensis</i>	-	x	x	-	-	-	-	-	-
	<i>Macrothrix hardingi</i>	-	x	x	o	o	x	x	r	x
	<i>Macrothrix</i> spp.	-	x	x	-	-	-	-	x	-
	<i>Neothrix</i> spp.	x	x	x	r	o	o	x	xx	o
	<i>Alona uacrocopa</i>	r	r	o	-	-	-	-	-	-
	<i>Alona rigidicaudis</i>	-	-	-	-	-	-	-	o	o
	<i>Chydorus hybridus</i>	x	-	x	-	-	-	-	-	-
	<i>Ephemeroporus tridentata</i>	x	x	x	o	o	o	-	-	-
	<i>Leberis aenigmatosa</i>	x	x	x	x	x	x	-	-	-
	<i>Planicirculus alticariuatus</i>	-	-	x	-	-	-	-	-	-
	<i>Plurispina multiluberculata</i>	xxx	xx	xx	-	-	-	-	-	-
	<i>Rak</i> sp.	xx	-	-	-	-	-	-	-	-
Copepoda	<i>Boeckella opaquua</i>	xxxx	xxxx	xxxx	xx	xx	x	-	xxxx	r
Ostracoda	<i>Bennelongia</i> spp.	xx	x	xx	x	-	xx	-	-	-
	<i>Candonocypris</i> spp.	xx	x	x	x	x	x	-	-	x
	<i>Cyprretta baylyi</i>	x	x	x	-	-	-	-	-	-
	<i>Cypricercus</i> spp.	xxx	-	xxx	xx	x	xxx	-	x	x
	<i>Ilyodromus anaplicolis</i>	xx	xx	xx	xx	xx	xx	xx	xx	x
	<i>Limnocytherae</i> spp.	-	x	o	-	-	-	-	-	-
	<i>Sarscypridopsis</i> spp.	xx	-	xx	-	-	-	-	-	-
Odonata	<i>Hemicordulia tau</i>	-	-	-	-	-	o	r	o	-
Hemiptera	<i>Micronecta gracilis</i>	-	r	r	r	-	r	-	o	-
	<i>Agraptocorixa parvipunctata</i>	-	o	-	r	o	r	-	o	-
	<i>Auisops gratus</i>	-	r	-	-	r	-	-	r	-
	<i>Auisops hyperion</i>	-	-	-	-	r	-	-	-	-
	<i>Auisops stali</i>	-	-	-	-	-	r	r	-	-
	<i>Auisops thienemannii</i>	r	-	o	r	o	r	-	x	-
Coeloptera	<i>Allodessus bistrigatus</i>	o	o	-	-	o	-	-	-	-
	<i>Antiporus gilberti</i>	-	r	-	-	r	-	-	-	-
	<i>Berosus</i> spp.	r	-	-	-	-	-	-	-	o
	<i>Enochrus</i> sp.	-	-	-	-	-	-	-	-	r
	<i>Eretes australis</i>	-	-	-	r	-	-	r	o	o
	<i>Megaporus howitti</i>	-	-	o	-	-	-	-	-	-
	<i>Paroster</i> sp.	-	-	-	x	o	xx	x	x	xx
	<i>Rhantus suturalis</i>	-	-	-	-	-	-	-	r	-
	<i>Sternopriscus multimaculatus</i>	r	x	x	xx	xxx	xx	x	xx	xx
	<i>Allodessus</i> larva	r	-	-	-	-	o	-	-	-
	<i>Antiporus</i> larva	-	-	-	-	-	-	o	-	-
	<i>Paroster</i> larva	o	o	-	x	o	x	x	x	x
	<i>Sternopriscus</i> larva	o	o	o	-	-	-	-	-	-
Tricoptera	<i>Triplectides australis</i>	-	-	-	-	x	-	o	o	-
	unidentified species	-	-	-	-	r	-	-	-	-
Diptera	juvenile chironomids	o	x	x	x	x	-	-	-	-
	<i>Allotrissocladius</i> sp.	x	o	o	-	x	-	r	xxx	xx
	<i>Chironomus lepperi</i>	-	-	-	-	-	-	-	o	-
	<i>Paraborniella toumoiri</i>	x	x	x	xx	x	x	xxx	xxx	xx
	<i>Parakeifferiella variagatus</i>	xx	-	-	-	-	-	-	-	-
	<i>Procladius</i> sp. (Pentaneurini)	o	-	o	r	-	-	-	r	x
	<i>Dasyhelea</i> sp.	x	x	x	r	x	o	x	x	-
	<i>Aedes albopunctatus</i>	-	o	-	-	x	-	x	-	o
	tipulid larvae	-	-	-	r	-	-	-	-	-
Mollusca	<i>Glyptophysa</i> sp.	-	o	o	-	-	-	-	-	-
	<i>Isidorella</i> sp.	-	o	-	-	-	-	-	-	-
Arachnida	oribatid mite	-	-	-	-	-	-	o	-	-
	trombidoid mite	-	-	-	o	x	o	o	r	r
Momentary Species Richness		30	33	34	26	28	26	19	27	21

Species frequencies: r, 0.1; o, 0.2–0.9; x, 1–3; xx, 3.1–9.9; xxx, 10–19.9; xxxx, >20.

APPENDIX 2 SPECIES LISTS FOR ROCKS ON EASTERN TRANSECT.

Major group	Species	McDermid	Banks	Disappointment	McPherson	Unnamed	Theatre	Afghan	Balladonia	Booanya
Turbellaria	unidentified black planarian	x	xx	xx	xx	x	-	x	x	xx
	unidentified green planarian	-	xx	-	xx	xxx	x	x	-	o
Nematoda	unidentified nematodes	-	r	o	-	o	x	-	xx	o
	<i>Hexarthra</i> sp.	-	-	-	-	-	-	-	-	o
Rotifera	<i>Branchinella basispina</i>	-	-	-	-	-	-	-	x	o
	<i>Branchinella longirostris</i>	x	xxx	x	o	xx	-	-	-	-
Branchiopoda	<i>Limnadia badia</i>	xxx	xx	xx	xx	xxx	xx	xx	xxx	xx
	<i>Lynceus macleayanus</i>	-	-	-	-	xx	xxx	-	-	x
	<i>Caenestheriella mariae</i>	x	xxx	x	xx	xx	xxx	x	-	-
	<i>Triops</i> n. sp.	-	-	-	-	-	-	o	x	-
	<i>Daphnia jollyi</i>	-	-	-	-	o	-	-	-	-
	<i>Daphnia queenslandicus</i>	-	-	-	-	-	-	-	-	x
	<i>Ceriodaphnia</i> sp.	xx	xx	x	xx	xx	xxx	-	-	-
	<i>Moina australiensis</i>	-	-	-	-	-	x	x	-	-
	<i>Macrothrix hardingi</i>	o	-	xxx	r	-	-	-	-	x
	<i>Macrothrix</i> spp.	-	-	-	-	-	-	-	-	-
	<i>Neothrix</i> spp.	x	x	x	o	-	r	x	-	o
	<i>Alona rigidicaudis</i>	o	o	o	-	o	x	o	-	-
Copepoda	<i>Alona</i> spp.	-	-	-	-	xx	-	-	-	-
	<i>Celsinotum</i> sp.	-	-	-	-	-	-	-	-	x
	<i>Chydorus hybridus</i>	-	-	-	-	-	-	-	-	r
	<i>Ephemeroporus tridentata</i>	o	o	-	-	-	-	-	-	-
	<i>Leheris aenigmata</i>	xx	x	r	-	x	-	-	-	-
	<i>Plurispina multituberculata</i>	xx	-	-	r	xx	-	-	-	-
	<i>Boeckella opauqua</i>	xx	xxxx	xxx	xxx	xx	xxx	xxxx	x	x
	cyclopoid	-	-	-	-	-	o	o	r	-
Ostracoda	Harpacticoid sp 674 (DEC)	r	-	-	-	-	o	-	-	-
	<i>Bennelongia</i> spp.	x	o	x	x	x	x	-	-	-
	<i>Cabanocypris nunkeri</i>	-	-	-	-	-	-	-	xx	-
	<i>Candonocypris</i> spp.	xx	xx	o	x	x	x	o	-	-
	<i>Cypretta baylyi</i>	-	-	-	-	-	-	o	-	-
	<i>Cypericercus</i> spp.	xxx	xxx	xxx	xx	xxx	xxx	xx	xx	xxx
	<i>Cyprinotus edwardsi</i>	-	-	-	-	-	-	-	-	x
	<i>Heterocypris</i> sp.	-	-	-	-	-	-	xx	xx	xx
	<i>Ilyodromus amplicolis</i>	xx	xx	xx	x	xx	xx	x	r	x
	<i>Limnocytherae</i> spp.	o	o	-	-	x	-	-	-	o
	<i>Sarscypridopsis</i> spp.	-	-	-	-	-	-	x	x	-

		35	33	28	26	30	28	30	2433
Odonata	<i>Hemicordulia tau</i>	0	x	-	-	-	-	-	-
	<i>Ischnura heterotricha</i>	-	-	-	-	-	f	f	-
	<i>Orthetrum caledonicum</i>	0	-	-	-	-	-	-	-
Ephemeroptera	Cleon sp.	-	-	0	-	-	-	-	-
Hemiptera	<i>Micronecta gracilis</i>	-	-	-	-	-	0	-	-
	<i>Agraptocorixa parvipunctata</i>	0	x	f	o	o	f	f	xx
	<i>Anisops gratus</i>	-	o	f	f	f	o	-	x
	<i>Anisops hyperion</i>	f	f	-	-	-	f	-	o
	<i>Anisops stali</i>	f	o	-	f	-	-	-	-
	<i>Anisops thienemannii</i>	o	o	f	-	o	x	f	xx
Coleoptera	<i>Allodessus bistrigatus</i>	x	-	-	o	o	-	-	-
	<i>Antiporus gilberti</i>	o	o	f	o	-	-	f	-
	<i>Berosus</i> spp. (mainly <i>B. uultans</i>)	o	o	-	f	f	-	-	-
	<i>Cybisier tripunctatus</i>	-	f	-	-	-	-	-	-
	<i>Enochrus</i> sp.	-	-	f	o	o	-	-	-
	<i>Eretes australis</i>	o	f	o	-	o	-	o	-
	<i>Hyphidrus</i> sp.	-	o	-	-	-	-	-	-
	<i>Limnoxenus zeakandicus</i>	f	-	-	f	-	-	-	-
	<i>Paroster</i> sp.	o	f	x	-	-	-	-	-
	<i>Sternopriscus multimaculatus</i>	xx	xx	xxx	xxx	xx	xx	xx	xx
	<i>Allodessus larva</i>	-	-	-	-	-	-	-	-
	<i>Eretes larva</i>	-	-	-	-	-	-	-	o
Tricoptera	<i>Paroster larva</i>	x	o	x	x	x	-	-	-
Diptera	<i>Tripsectides australis</i>	f	o	o	-	o	-	-	-
	juvenile chironomids	-	o	o	-	-	-	-	-
	<i>Allotrissocladius</i> sp.	-	x	xxx	-	-	-	-	-
	<i>Chironomus tepperi</i>	-	-	-	-	-	-	-	xx
	<i>Paraborniuella touvoiri</i>	x	x	xx	xx	xx	-	o	f
	<i>Procladius</i> sp. (Pentaneurini)	x	-	f	-	f	o	-	o
Mollusca	<i>Dasythelea</i> sp.	o	-	-	x	o	xxx	xxx	o
	<i>Glyptophysa</i> sp.	-	-	-	-	-	-	-	o
Arachnida	<i>Isidorella</i> sp.	-	-	x	-	xx	-	x	-
	hydrocarinid mite	-	-	-	-	-	-	-	f
	trombidoid mite	-	-	-	-	-	-	-	-
Montemporary Species Richness		35	33	28	26	30	28	30	2433

Species frequencies: r, 0.1; o, 0.2–0.9; x, 1–3; xx, 3.1–9.9; xxx, 10–19.9; xxxx, >20.